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REPRODUCTION AND GROWTH OF THE SMOOTH PEBBLE CRAB *PHILYRA LAEVIS* (Bell 1855) AT TWO SITES IN SOUTH AUSTRALIA DURING 1990-91.

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Summary

McKILLUP, S.C. & McKILLUP, R. V. (1994) Reproduction and growth of the smooth pebble crab *Philyra laevis* (Bell 1855) at two sites in South Australia during 1990-91. *Trans. R. Soc. S. Aust.*, **118**(4), 245-251, 30 November, 1994.

The growth and life history of the smooth pebble crab *Philyra laevis* (Bell) was inferred from collections made between July 1990 and December 1991 from Sultana Point and Coobowie, South Australia. *P. laevis* appeared to be semelparous and to reproduce twice a year at both sites. At Sultana Point ovigerous females were common in winter (June-July) and from late spring to late summer (November-February). Dead adults were common from late winter to early spring and also in early summer. Distinct cohorts of new recruits were found in early spring and again in early summer. Recruits grew rapidly, reaching sexual maturity within four months. The mean size of adult females and the proportion which were ovigerous differed amongst populations. A laboratory experiment showed that food availability affected growth and whether females became ovigerous. We postulate that differences in size and ovigery amongst populations of *Philyra laevis* may be caused by differences in the availability of food.

KEY WORDS: *Philyra*, pebble crab, life-history, intertidal, food, sandflat.

Introduction

The smooth pebble crab, *Philyra laevis* (Bell 1855), is common on sheltered intertidal sandflats in southern Western Australia, South Australia, Tasmania and Victoria (Phillips *et al.* 1984). Hale (1976) describes the feeding and courtship behaviour of *P. laevis*, but little else is known about this crab. Tasmanian populations of *P. laevis* have been reported to host a nemertean (genus *Carcinonemertes*) (Bell & Hickman 1985) and the trematode *Microphallus paragrapsi* Smith, 1983 (Bell 1988). From 1990-91 we studied the feeding behaviour of *Philyra laevis*, finding that although individuals often fed upon other dead or damaged animals, many were unwilling to feed upon members of their own species and that water borne cues from damaged *P. laevis* inhibited feeding (McKillup & McKillup 1992). During the study, we collected *P. laevis* over an 18-month period from two sites 10 kilometres apart in South Australia, and also sampled 10 other southern Australian sites. These data, together with results of a laboratory feeding experiment, are used to infer the life history of *P. laevis*.

Methods

Sampling of Philyra laevis *from Sultana Point and Coobowie*

Samples of *Philyra laevis* were collected from the intertidal sandflat at Sultana Point, lower Yorke Peninsula, South Australia (35.08°S 137.44°E) in July 1990, and then approximately every four weeks from September 1990 to August 1991 and in December 1991. The sandflat at Coobowie Bay, 10 km north of Sultana Point, was sampled in the same way but less frequently (November 1990 and January, March, April, August and December 1991).

P. laevis is active whilst the sandflat is covered by water during ebb and rising tides, but remains buried in the substratum at high water or when the sandflat is completely exposed (Hale 1976). At least 30 and usually more than 100 individuals were collected from within the intertidal zone where *P. laevis* occurred (from low water to about mid tidal level) between the time of low water and when the sandflat was inundated by the rising tide. At each site at least 160m^2 of substratum, consisting of several haphazardly chosen 0.5 metre wide strips from the water's edge to mid tide level, were hand searched to a depth of 3.5 cm. *P. laevis* was found no deeper than 3.0 cm in the substratum (McKillup & McKillup unpubl.). Crabs were frozen and later examined for sex, whether females were ovigerous, and the carapace width of all individuals was measured to the nearest 0.05 mm.

Reproductive condition and average size of adult females at additional sites

During January and February 1991, at least 75 *Philyra laevis* were collected from each of 11 sites in South Australia and one in Victoria (Swan Bay within Port Philip Bay), and examined for sex, size and reproductive state as described previously.

Laboratory experiment on sexual development and growth

Abdominal morphology in the Crustacea can usually be used to determine sex: adult males often have a relatively narrow, concave sided and tapered abdomen, whilst females have a broader and often circular abdomen almost as wide as the carapace (Hartnoll

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Fig. 1. Abdominal morphology of *Philyra laevis*. From left to right: male, intermediate (= juvenile female) and adult female.

1982). This was the case for all *Philyra laevis* with carapaces wider than 13.5 mm, but three morphological types were found in crabs 13.5 mm wide or smaller: the two previously described forms, plus individuals with a convex sided abdomen which, at its widest point, was approximately half the width of the carapace (Fig. 1). The last described individuals were named "intermediates".

The growth of 20 females, 20 intermediates and 20 males, all of carapace width 10.5 mm or less, was observed in the laboratory. Considering that we also found differences in the size and proportion of adult females which were ovigerous amongst sites, and that differences in adult size amongst (unspecified) localities were also reported by Hale (1976), observations were made as part of a manipulative laboratory experiment designed to examine the effects of food availability upon growth and egg production of *Philyra laevis*. Crabs were placed individually in 50 x 50 x 30 mm deep plastic dishes, each filled with 40 ml of seawater. All individuals were numbered on the dorsal side of their carapace with non-toxic waterproof ink. Six dishes, containing two males, two females and two intermediates were placed within each of 10 lidded 280 × 380 × 110 mm deep plastic trays containing seawater to a depth of 10 mm. Aeration was not needed. The seawater in the trays maintained a high level of humidity which reduced evaporation from the dishes and also provided a marine environment for the few crabs which climbed out during the experiment. Trays were kept at room temperature and natural day length.

Five trays were assigned randomly to a "high food" treatment and the 30 crabs within these were fed every working day (from Monday to Friday), whilst the 30 crabs in the other five trays were fed weekly, on Wednesdays, as a "low food" treatment. Different frequencies of feeding provide different levels of food availability to invertebrates (e.g. Calow 1973; Moriarty 1978). For each feeding the six crabs in a tray were removed, placed in six separate dishes used for feeding only and offered *ad libitum* crushed cockle, *Katelysia scalarina* Lamarck, from Sultana Point. *P. laevis* is often found feeding on this bivalve in the field (McKillup & McKillup 1992). All crabs fed for 12 min or less and were returned to their permanent dishes after 15 min. This method of feeding prevented the seawater in the permanent dishes from becoming fouled; it was replaced fortnightly. Crabs were inspected on every working day, individuals which had moulted were examined and sexed as either male, female or intermediates, and any which had climbed out were replaced in their dishes.

The experiment began on April 2nd 1991 using new recruits from the December 1990 - January 1991 cohort at Coobowie, and continued until all crabs had moulted at least once.

Results

Sampling of Philyra laevis *from Sultana Point and Coobowie*

The size structure of the population of *Philyra laevis* at Sultana Point from July 1990 to December 1991 is illustrated in Figs 2, 3. In mid-winter (July 1990), all males were at least 8.5 mm wide, all females at least 7.5 mm wide and 93% of the latter were ovigerous. By early spring (September 1990), dead males and females were extremely common and large live individuals were not; almost half of the live males collected were smaller than 8.5 mm and appeared to be a distinct cohort of recent recruits. Only two live adult females were found; both were more than 7.5 mm wide and ovigerous. The remainder of the sample consisted of "intermediates" 7.5 mm wide or smaller, which were not present in the July sample. A laboratory experiment showed that intermediates were juvenile females (see below). In mid-spring (October 1990) only one cohort of males was present, and these males were larger than the recruits first seen in the previous month. The juvenile females were also larger and some relatively small adult females were present, but none was ovigerous. In late spring (November 1990), no juvenile females were found; the sample consisted of adult females at least 9.5 mm wide, 89% of which were ovigerous, plus males from 4.5 to 18.5 mm wide. In early summer (December 1990) another cohort of relatively small males was present, together with a cohort of juvenile females up to 9.5 mm wide. Dead adults were again common, but live adults were also found and 71% of adult females were ovigerous. The small males and juvenile females continued to grow through summer and autumn (January to April 1991) and the number of ovigerous adult females declined (30.6% in January, 14% in February and 5.6% in March). From mid- to late-autumn (April and May 1991) no juvenile females were found and only 1.5% and 2% respectively of adult females were ovigerous, but in early winter (June 1991), the percentage of ovigerous females had risen to 68% and further increased to 94% by late winter (July 1991). The early spring (August 1991) sample was very similar to that of September 1990; dead adult males and

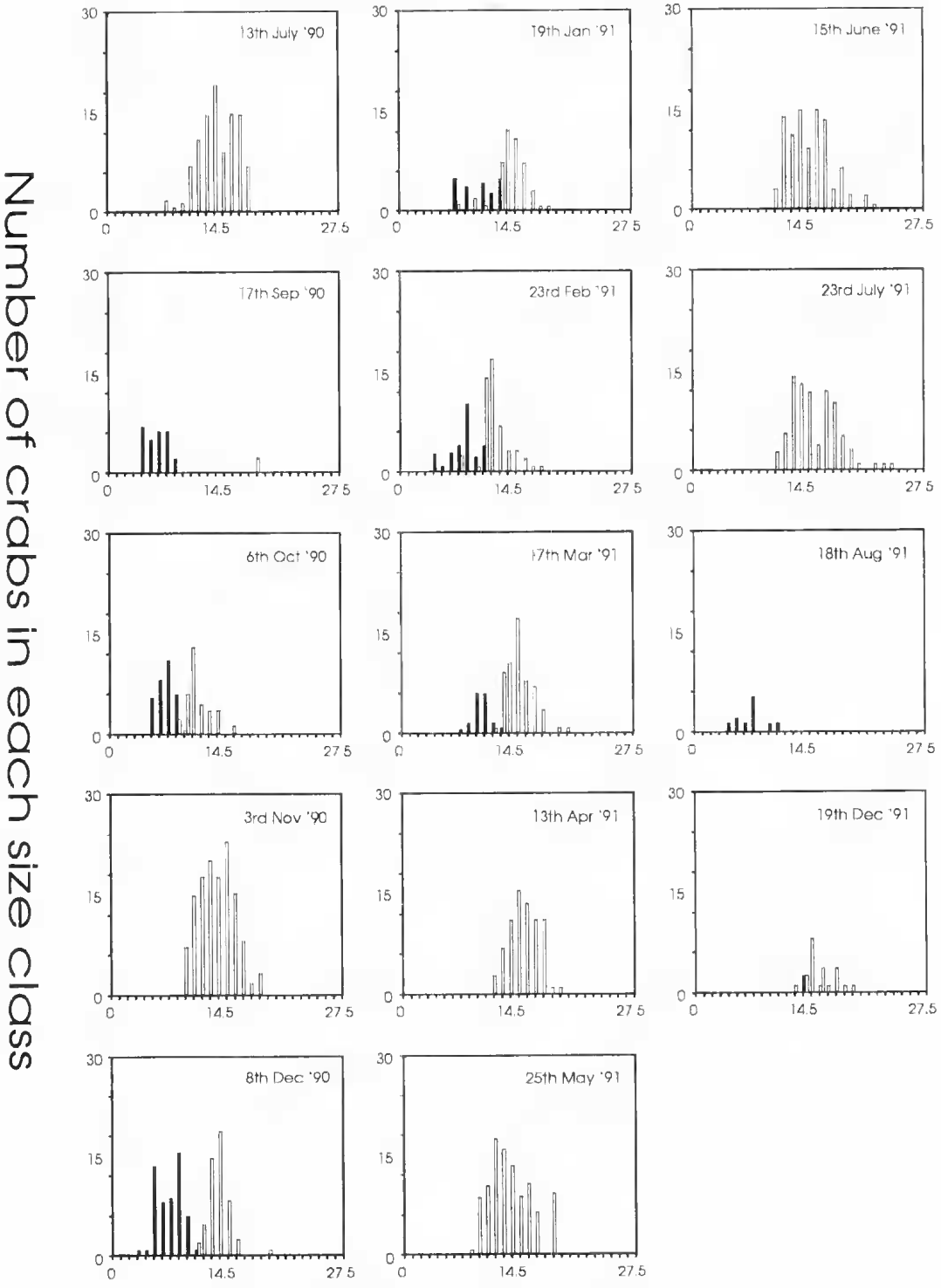

Fig. 2. The size structure of female *Philyra laevis* collected from Sultana Point, South Australia on 14 occasions between July 1990 and December 1991. Solid bars indicate juveniles; open bars, adults.

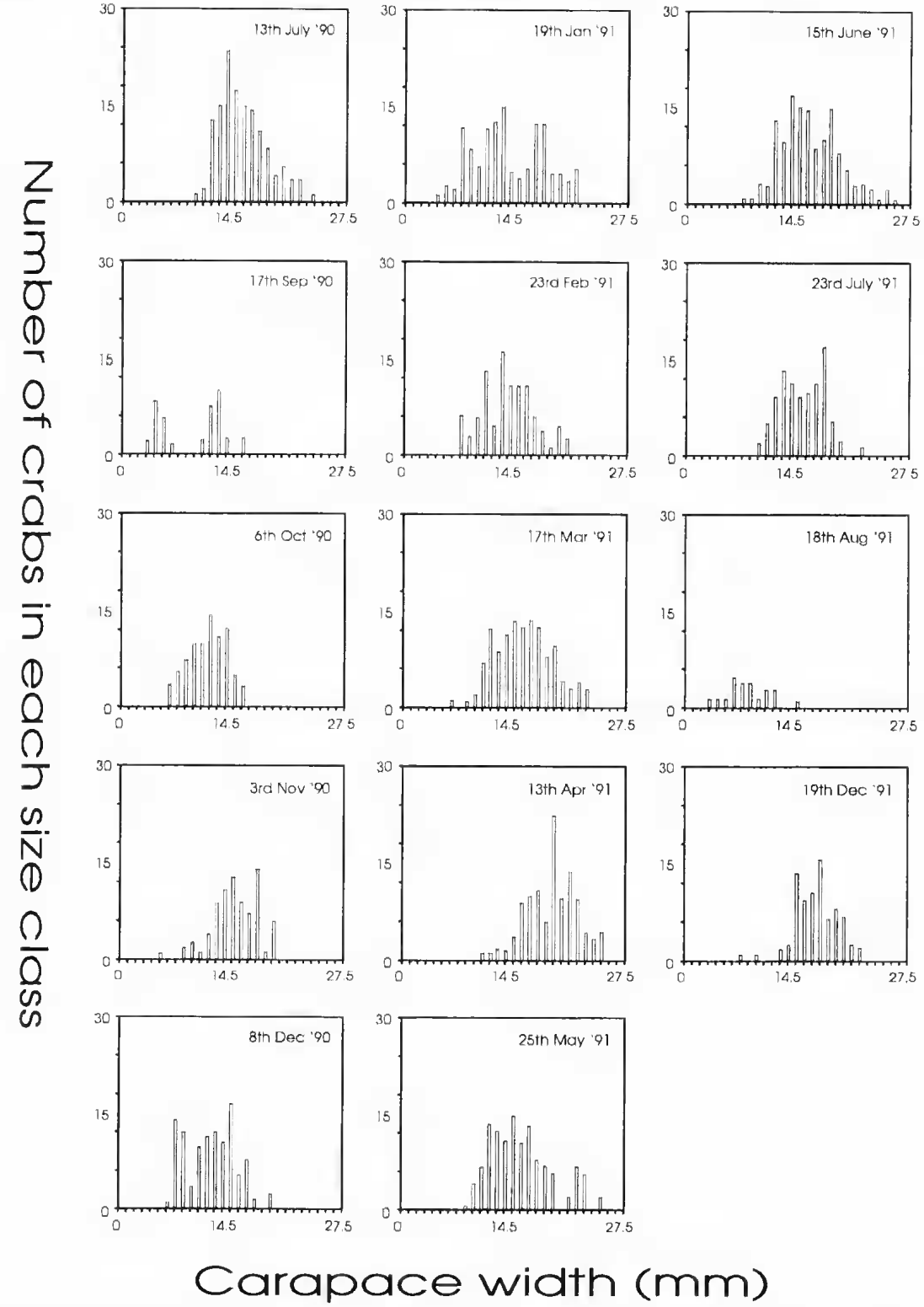

Fig. 3. The size structure of male *Philyra laevis* collected from Sultana Point, South Australia on 14 occasions between July 1990 and December 1991.

females were common and the sample of live *Philyra laevis* consisted entirely of juvenile females less than 8.5 mm wide and males which were almost all smaller than those collected during the previous month. The December 1991 sample was similar to the one from the previous December, consisting of adult males plus adult and some juvenile females, with 65% of adult females ovigerous. Dead adults were again common on the sandflat at Sultana Point in December 1991.

The data for Coobowie were consistent with those from Sultana Point. In late spring (November 20th 1990) only males and adult females were found, but in mid summer (January 19th 1991) juvenile females were also present and dead males and adult females were common. The average carapace width of the cohort of juvenile females present in early autumn (March 17th 1991) was larger than in January and most appeared to have moulted to adults by April 13th 1991. In late winter (August 18th 1991) dead adults were common and juvenile females plus small males were present. In early summer (December 19th 1991) dead adults were also found, very few live adult females were present and juvenile females were common.

The mean carapace width of adult females was always greater at Sultana Point than Coobowie (Table 1) and a greater proportion of adult females was ovigerous at Sultana Point than Coobowie on five occasions when comparison was possible (Table 2). Males were not compared since it was impossible to distinguish between juveniles and adults.

TABLE 1. *Comparison of the mean carapace width (in mm) of adult female* Philyra laevis *from Coobowie and Sultana Point. The November collections were made 17 days apart; on the other 5 occasions crabs were collected from both sites on the same day.* $\bar{x}$ = *mean,* s_x = *standard deviation and* n = *sample size.*

	Site					
	Coobowie			Sultana Point		
Date collected	n	$\bar{x}$	s_x	n	$\bar{x}$	s_x
November 1990	33	9.23	2.37	125	13.17	2.02
19 January 1991	17	12.74	1.75	49	13.19	1.73
17 March 1991	52	12.62	1.42	71	13.68	1.72
13 April 1991	85	13.18	1.75	65	14.19	1.77
18 August 1991	22	11.82	1.94		none found	
19 December 1991	9	11.72	1.72	22	13.50	1.83

TABLE 2. *The number of adult female* Philyra laevis *and those ovigerous in samples collected from Coobowie and Sultana Point on 6 occasions during the same month. The November collections were made 17 days apart; on the other 5 occasions crabs were collected from both sites on the same day.*

	Site			
	Coobowie		Sultana Point	
Date collected	Collected	Ovigerous	Collected	Ovigerous
November 1990	33	1	128	119
19 January 1991	17	0	49	15
17 March 1991	52	0	71	4
13 April 1991	89	0	65	2
18 August 1991	22	15	0	–
19 December 1991	9	0	22	14

TABLE 3. *The percentage of ovigerous adult female* Philyra laevis *at 12 sites sampled during January and February 1991, together with the mean carapace width of adult females from each site.*

Date sampled	Site	Number of mature females collected	Number and percentage ovigerous		Mean carapace width of females (mm)
19 January 1991	Edithburgh Bay	9	0	(0)	12.67
19 January 1991	Sultana Point	49	15	(31)	13.19
19 January 1991	Coobowie	17	0	(0)	12.74
19 January 1991	Hickey's Point	25	2	(8)	13.10
19 January 1991	Stansbury	33	7	(21)	14.35
20 January 1991	Point Turton	3	0	(0)	14.83
20 January 1991	Rogues Point	86	6	(7)	13.90
29 January 1991	James Well	20	1	(5)	12.65
29 January 1991	Pine Point	23	1	(4)	12.33
2 February 1991	Foul Bay	87	0	(0)	13.89
2 February 1991	Sturt Bay	70	10	(14)	13.10
13 February 1991	Swan Bay (Vic.)	66	56	(85)	17.46

Reproductive condition and average size of females at additional sites

Data for the number of adult females collected and the number and percentage which were ovigerous for 12 populations sampled in mid to late summer 1991 are in Table 3. The percentage of ovigerous females decreased at Sultana Point from January to February, so only samples collected on the 19-20th January 1991 were compared statistically. Nevertheless, the proportion ovigerous differed significantly amongst the seven sites sampled on lower Yorke Peninsula (2 × 7 contingency table comparison: $df = 6$, Chi-squared statistic = 22.26, $P < 0.005$). The significant heterogeneity amongst sites was largely due to the greater proportion of ovigerous females at Sultana Point (Table 3). Considering all sites sampled, the highest percentage of ovigerous adult females (85%) was at Swan Bay, Victoria during early February (when only 14% were ovigerous at Sultana Point; see earlier discussion of Figure 1). The Swan Bay population also contained the largest *Philyra laevis* found. Furthermore, for the seven sites sampled from the 19-20th January (excluding Point Turton where only three females were collected), ovigerous females were found only at sites where the average carapace width of females was greater than 13.00 mm (Table 3).

Laboratory experiment on sexual development

Male, adult female and "intermediate" *Philyra laevis* offered food on five of seven days per week moulted sooner than those only fed once per week (Table 4). At their first moult in the laboratory all males moulted to males, all females to females and all intermediates to females, except for the two smallest which remained as the intermediate form until they moulted again. In all cases the variance of days elapsing before moulting was greater in the low food treatment, and by inspection the distributions in this treatment were skewed to the right. None of the adult females in the low food treatment, but all in the high food treatment, were ovigerous by July 1991.

Discussion

Philyra laevis reproduced twice a year at Sultana Point and death of most adults during the breeding months suggests this species is largely semelparous. Recruits found in early spring (September 1990) reached sexual maturity and reproduced from late spring to late summer (November 1990 to February 1991), while those first found in early summer (December 1990) reached sexual maturity by mid-autumn (April 1991) and reproduced until early winter (June 1991). Data from Coobowie were consistent with this pattern of recruitment, but suggest that many adult *P. laevis* at Coobowie did not reproduce in the summer of 1990-91, although data were scanty, being only for November 1990 and January 1991.

Recruits were found one month after reproducing females were present in late spring and two months after they were present in early winter. Considering that the sandflat was only sampled monthly, that the smallest crab found was 2.8 mm (McKillup & McKillup unpubl.) and that smaller individuals were likely to be overlooked amongst sand grains and detritus, the larval stage of *P. laevis* is likely to be of relatively short duration (perhaps only 1-2 weeks). Another member of the same genus, the purse crab *Philyra globosa* (Fabricius), has a larval stage lasting 11 days in the laboratory at an average temperature of 28°C (Krishnan & Kannupandi 1990).

The moult from juvenile to adult form in females appears to coincide with sexual maturity, since only two females with juvenile abdomens of more than 300 examined were ovigerous (McKillup & McKillup unpubl.). A relative ("non-allometric") increase in abdomen compared to carapace width during the moult to adulthood is common in brachyurans (Hartnoll 1974).

For sites sampled from the 19-20th January 1991, a greater proportion of ovigerous adult females was present where the mean carapace width of females was relatively large. Also, there was a greater proportion of ovigerous females at Sultana Point than Coobowie on all occasions when comparison was possible. Differences amongst sites were not caused simply by larger females being more likely to be ovigerous; examination of the data used to compile Table 2 showed that in November, 60 of 69 adult females between 8 and 13 mm wide were ovigerous at Sultana Point, but none of 19 collected on the same date and within the same size range was ovigerous at Coobowie. Furthermore, on January 19th 1991, none of the 17 adult females collected from Coobowie was ovigerous, even though the carapace widths of these individuals were

TABLE 4. *The mean days elapsing before* Philyra laevis *first moulted in high and low food treatments.* $\bar{x}$ = *mean,* s_x = *standard deviation,* n = *sample size.*

	Treatment					
	High Food			Low Food		
	n	$\bar{x}$	s_x	n	$\bar{x}$	s_x
Males	10	24.10	3.78	10	39.10	17.10
Females	10	23.5	7.38	10	45.20	25.33
Intermediates	10	23.00	10.79	10	38.10	21.81

within the size range of the 15 ovigerous females collected from Sultana Point. Similarly, on December 17th 1991, none of 9 adult females from Coobowie was ovigerous, even though six were within the size range of ovigerous females from Sultana Point.

Results of the laboratory experiment were consistent with food supply affecting the frequency of moulting. A sample of crabs will contain individuals at different stages of the moult cycle. In the low food group, crabs about to moult would have done so soon after the experiment began, but those which had moulted shortly before being collected would have to prepare to moult again under the laboratory conditions of low food availability. In contrast, in the high food group, crabs prepared to moult would do so, and others which had recently moulted would have adequate resources available to grow and moult again. This can explain the greater mean, variance and positive skew of the number of days before moulting in the low compared to the high food treatment (Table 4).

We suggest, for the following reasons, that differences in size and the proportion of ovigerous adult females amongst sites were caused by differences in food availability. Firstly, in the laboratory, crabs in the high food treatment moulted sooner (and therefore grew faster) than those in the low food treatment, and only females in the high food treatment produced eggs. Secondly, adult female *P. laevis* at Coobowie were consistently smaller than those at Sultana Point. The intertidal scavenger *Nassarius pauperatus* (Lamarck), a prosobranch snail which occupies a similar niche and is often found feeding with *Philyra laevis*, is also smaller (and hungrier) at Coobowie than at Sultana Point, and we have postulated there is less food available to *N. pauperatus* at Coobowie than at Sultana Point (McKillup & Butler 1979, 1983; McKillup 1983). Furthermore, we have more recently postulated that intertidal scavengers may generally be short of food (McKillup & McKillup 1994). All South Australian populations of *P. laevis* sampled contained smaller females on average than the population at Swan Bay Victoria, suggesting that food availability may be limiting the growth and reproduction of many populations of this scavenger. Notably, females of another leucosiid crab, *Ebalia laevis* (Bell, 1855) were only found ovigerous during December, January, May and August at Wellington, New Zealand, but records from other localities suggest the duration of the reproductive season varies amongst sites (Wear & Fielder 1985).

The hypotheses that differences in food availability are limiting the duration of the reproductive period of *Philyra laevis* and that individuals in natural populations of this species are short of food could be tested by frequently feeding marked individuals in the field and comparing their growth and reproductive output with the rest of the population. The results of these experiments may explain why *Philyra laevis* has a relatively short lifespan and two seasonally opposed breeding seasons in South Australia.

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